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Wound periderm in certain cacti

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(WITH PLATE 9 AND THREE TEXT FIGURES)

NORMAL TISSUE

The two cacti upon which the work of this paper is based are *Opuntia versicolor* Engelmann and *O. discata* Griffiths. These are jointed, branching forms, characteristic of the flora in the vicinity of Tucson, Arizona. Morphologically they differ in that the joints of the *O. versicolor* are composed of fluted cylinders, while those of the *O. discata* are more or less disc-shaped. Necessarily, a cross section of the former presents the appearance of a circle with an undulating margin, while one of the latter is more of an elongated ellipse. Anatomically considered, they are identical in all essentials. There is (1) a distinct pith in the center, bounded (2) by a ring of bundles equidistant from the exterior; outward from the bundles (3) a ring of cortical tissue, which extends to the (4) hypoderm, outside of which is the (5) epidermis. Subepidermally, in plants several years old, normal periderm occasionally, but not typically, forms in isolated areas.

Schleiden (3), in his early work on the cacti, describes fairly accurately several forms, which, however, do not include either *O. versicolor* or *O. discata*.

A further discussion of the tissues in their normal condition is prerequisite to a complete understanding of their behavior as a result of wounding.

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The pith is composed of thin-walled, isodiametric cells, loosely packed together, and with consequent large intercellular spaces. The cells themselves contain, aside from the usual protoplasmic contents, a considerable quantity of stored starch, and small crystals of calcium oxalate. These crystals are found in large quantities in practically all of the tissues of both opuntias, sometimes causing, parallel with their own growth, an hypertrophy of the cells containing them. In a concentrated solution of hydrochloric acid, the calcium oxalate of a medium-sized crystal does not dissolve for over half an hour. Lauterbach (2) describes these crystals as being star-shaped clusters composed of monoclinic prisms, which have a short principal axis, and states that they make up 85 per cent. of the weight of the ash.

The bundles vary somewhat in their structure with the age of the plant and their position in the stem. Essentially, they are of the open collateral type, with hadrome and leptome on the same radius, separated by a cambial layer. The hadrome, much greater in extent than the leptome, consists of annular and spiral ducts, occasional parenchyma cells, and, in many cases, large interspersed masses of stereome tissue. The ducts and stereome cells are lignified, as shown by testing with phloroglucin and hydrochloric acid, and in cross section the latter greatly resemble the median optical view of the lignified-walled cells, to be described later in the formation of the periderm. The cells of the cambial region, as seen in cross section, present the typical brick-shaped appearance, and form, at the most, a layer not more than three or four cells deep. The leptome is composed of the characteristic sieve tubes and their accompanying companion cells, interspersed with parenchyma tissue. In cross section the peripheral portion of the leptome mass appears dome-shaped, and is capped by a mass of collenchymatic cells which resemble those of the hypoderm, referred to later on. The walls of these cells often become more or less mucilaginous, an occurrence similar to that found by Lauterbach (2, p. 262) in *Pereskia*, also one of the Cactaceae. The subcortical cells in the bundle region appear isodiametric, like those of the pith. However, there is a gradual merging of these cells with those in the outer cortical region, which are distinctly cylindrical and arranged end on end, with their long axes at right angles to the periphery. The outer five or six rows are normally rich in chloroplasts, and practically all of the cortical tissues contain a plentiful supply of stored starch. In seedlings a single-layered epidermis covers the distinctly parenchymatic cortical cells. However, as the plant matures, the outer cortex gives rise to a clearly differentiated tissue, the hypoderm, socalled by Solereder in his Systematic Anatomy of the Dicotyledons (**4**). The cells of the hypoderm are, in both opuntias here studied, from five to seven layers in depth, and decidedly collenchymatous in character. Schleiden (**3**, p. 348) describes this condition as arising through loss of water, from cells originally mucilaginous. PLATE 9, FIG. 1 will serve to give an idea of the thick cellulose walls, traversed by pit canals which radiate out from the comparatively small lumina, indicating protoplasmic continuity between the cell contents. The outer layer, which lies just underneath the epidermis, is characteristically so filled with oxalate crystals as to almost obliterate the walls. Occasional crystals are found in the other cells. This tissue has been described for different species of *Opuntia* by Lauterbach (**2**, pp. 259–264), as well as by the two authors mentioned above.

The epidermis is a single layer of cells in thickness and covered thickly with cutin, as shown by staining with Sudan III and heating. The stomatal openings extend through the hypodermal tissue down to the cortical cells. The guard cells are somewhat sunken, and the whole cavity is lined with cutin continuous with that on the outside. This fact was brought out by Mohl (see Solereder, **4**, p. 408) in his work on the cacti.

The normal periderm, mentioned in the introduction as forming in plants several years old, arises superficially, and gives the appearance of circular markings on the surface. When examined in a transverse section of the stem, it is seen to be composed of alternating zones of thin- and thick-walled tissue, each zone being itself several layers of cells in thickness (PLATE 9, FIG. 6). The thin-walled cells appear brick-shaped, and superficially greatly resemble meristematic tissue, except that their walls are highly suberized. The thick-walled cells are, on the contrary, lignified, reacting with phloroglucin and hydrochloric acid as did the stereome mentioned in discussing the structure of the bundles.

A single layer of this lignified tissue is never deeper than three cells, arranged one on top of another; the outer tangential and the radial walls are thicker than the inner tangential ones, and in consequence the peripheral portions of the lumina are dome-shaped, as is so common in thickened cutinized tissue of the epidermis. In very thin sections stained with Bismarck brown, distinct striations can be seen in the walls, coarser near the lumen, and becoming finer toward the exterior; while running at right angles to these striations are numerous fine pores. PLATE 9, FIG. 5, gives an optical transverse view of this tissue. The middle lamellae are shown, but the striations and pits above referred to are not indicated. In describing the origin of this particular tissue, Schleiden (3, p. 352) says that there arises a thick, yellow-brown, granular, slimy mass, in which eventually cells are formed. At present such an hypothesis is not to be accepted. However, although omitting any reference to lignification, he brings out clearly the fact that in the mature periderm there are alternating zones of suberized thin- and thick-walled tissue.

EFFECT OF WOUNDING ON NORMAL TISSUE

Having studied the normal tissues, with especial reference to the periderm, the next problem was to find out what reactions would follow as a result of injury. Wounds were brought about by making longitudinal slits down the plants with a razor, usually cutting deeper than the bundle ring, but never beyond the center of the pith. A contraction of the cells near the cut surface resulted, thereby opening up the wound, and exposing the tissue to the air. After the elapse of definite periods this material was placed in alcohol. Some stems were wounded with glass, in order to avoid a possible stimulus which might result from the acids of the tissues acting on the steel of the razor, and the resultant formation of soluble iron salts. In running a parallel series, however, there was found to be no difference in the rate of wound reaction between the two, so the use of the razor was adhered to.

All of the material used came originally from Tucson, Arizona. In the spring of 1913, cuttings were sent from Tucson, which were immediately wounded and killed, but gave unsatisfatory results. Plants from Tucson were wounded while growing in the Barnard

College greenhouse, but, although giving fairly good results, they were by no means as dependable as those obtained from material wounded and killed directly in its natural habitat in Tucson. Material of this character, collected by Dr. H. M. Richards in 1911 and by Dr. D. T. MacDougal in 1914, serves as the basis for the observations which follow.

Practically all of the studies have been made from transverse sections through the stems, where, owing to the above mentioned opening of the wound, the two exposed surfaces form a "V." Hand sections stained with Bismarck brown served to show clearly all cell walls, and the unstained portions were easily tested for cutin, cellulose, lignin, etc. Although most of the figures were made from such hand sections, those cut with a microtome were used for reference.

The only visible change during the first day after wounding is the partial loss of starch in a region running parallel with the exposed surface of the wound, but not bordering directly upon it. By the second day, that region is entirely starchless, and the reaction with iodine of the starch in the cells on the wound surface does not give the normal purplish blue, but more of a reddish color, suggesting the presence of a greater proportion of erythrodextrin.

In three-day-old wounds, some of the oxalate crystals in the most exposed cells have increased in size. The starchless area in the upper part of the "V" has become divided into two practically equal parts, by the foreshadowing of a meristematic layer running parallel to the surface of the wound. The cells in the outer region, that is, between this future meristem and the cut surface, are somewhat discolored. The cells comprising this prospective wound-phellogen are one layer in depth, and although no divisions have as yet taken place, there seems to be an adjustment of the containing cytoplasm to form a flat plate, continuous from one cell to another, and parallel to the wound surface. PLATE 9, FIG. 2, will give an idea of how this appears in section.

A wound four days old shows the meristematic or phellogen layer more clearly, especially near the periphery, where the cells seem about to divide. Near the base of the cut, particularly if the wound is deep and the circulation of air slight, it is undeveloped, possibly due to lack of available oxygen or perhaps to the lessening of the transpiration. See TEXT FIG. 1. The latter is suggested by a fact mentioned by Küster (1, p. 187), that a preliminary condition for the production of wound-cork is that at least a small degree of transpiration must be possible for the exposed tissue. Here, as pointed out, the cells on the cut surface near the periphery must have at least a normal amount of transpiration, while those deep in the cut can have much less.

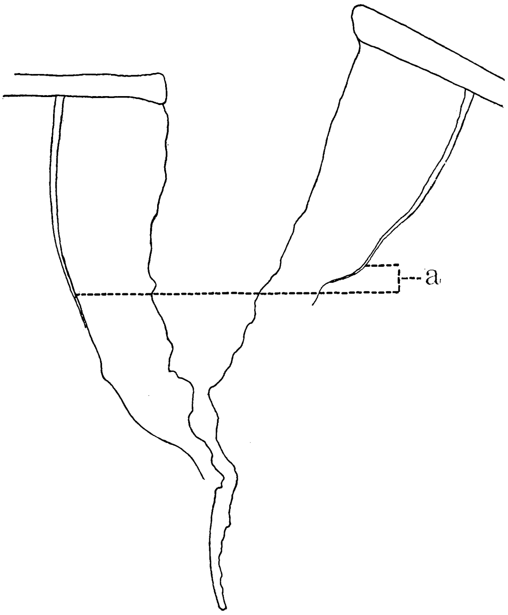

FIG. 1. Cross section of a four-day-old wound of an *Opuntia discata* plant, showing the characteristic V-shaped cut and the formation of the wound-phellogen only in the outer parts of the wound, × 28. *a*, phellogen layer.

Another change from the three-day-old wound is that the walls of the discolored cells nearest to and outside of the developing phellogen, have become lignified.

A study of a five-day-old wound can best be made by referring to TEXT FIG. 2. The phellogen is clearly distinguishable and has produced, except near the periphery, what may be spoken of as a distinct phellem. This phellem is about three cells deep, and the walls are highly suberized. The lignified cells just outside

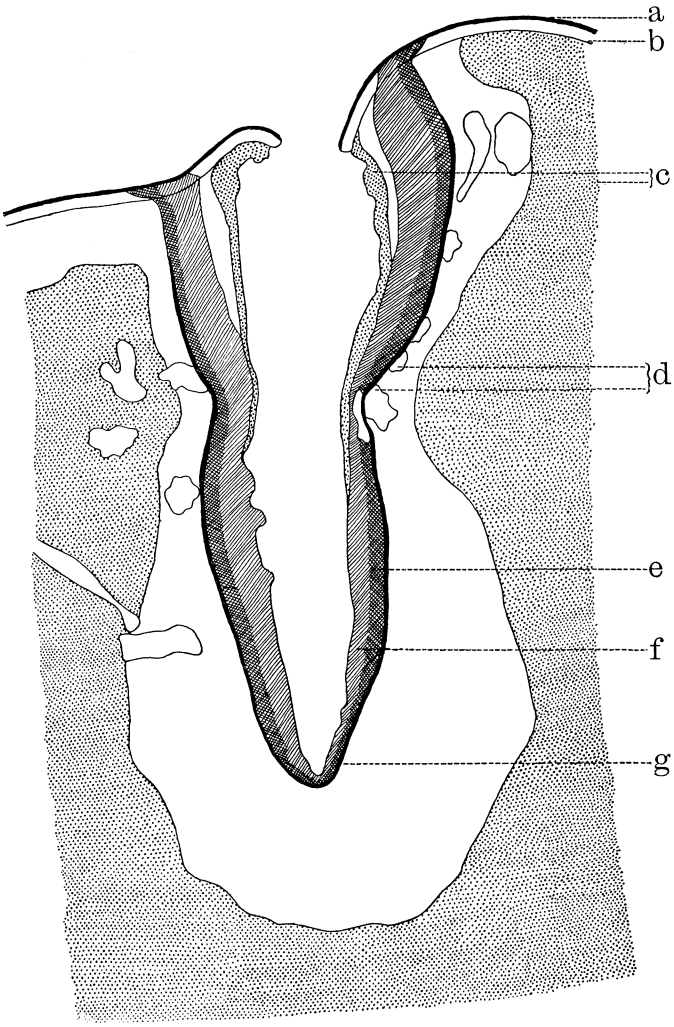

FIG. 2. Diagrammatic cross section through a five-day-old wound of an *Opuntia versicolor* plant, × 24; the open white areas consist of normal cellulose-walled cells; starch is found only in regions indicated. *a*, epidermal cells, with heavily cutinized outer walls; *b*, hypodermal tissue; *c*, cellulose-walled cells, containing stored starch; *d*, vascular bundles; *e*, cells, the walls of which have become discolored and lignified; *f*, cells, the walls of which have become discolored; *g*, suberized, thin-walled cells, produced through action of the first wound-meristem.

of them also give the suberin test, leaving, however, the large number of discolored cells unlignified, or giving the lignin test and no other. This phenomenon of cell walls giving the tests for both suberin and lignin Küster (1, p. 165) finds in the callus tissue of poplar cuttings. He says he does not doubt that the same substance, or a similar one, is the cause of these reactions. However, this statement is perhaps open to question. There seems no reason why both suberin and lignin might not be present together.

In wounds six and seven days old the phellogen has produced on the outside more suberized-walled phellem cells and on the inside what may be called a distinct phelloderm, the walls of which are pure cellulose (PLATE 9, FIG. 3). For the sake of convenience these tissues will be spoken of as phellem, phellogen and phelloderm, with the realization that, although analogous to the normal periderm of plants, they are not necessarily homologous. Although the phellem extends up through the hypoderm, few cells have been produced there. At this stage, still more of the cells in the discolored tissue have become lignified.

A wound ten days old shows several marked advances. The periderm is in all about eighteen cells deep. However, the phellogen, instead of producing only suberized phellem tissue, has given rise to a few thick-walled lignified cells, five or six in a cross section, appearing on one side, about half way down the "V." These cells were previously described in discussing the normal periderm. A further lignification of the discolored tissue is apparent. Another change is in the distribution of the stored starch. With the formation of waterproofing cells covering the wound, the normal activities of the tissues seem to be resumed, and small grains of storage starch appear in the phelloderm cells, and in the cortical cells below the phelloderm. These grains are, however, very few and very scattered.

The next wound studied in detail was twenty-four days old. Considering the various zones of tissues which extend from the wounded surface into the interior of the plant, we have (1) on the outside, the cells, in no way discolored, which retain the original stored starch they contained at the time of wounding. Some enclose oxalate crystals which have increased considerably in size.

Within is (2) the layer of discolored cells whose protoplasmic contents appears to have degenerated and the walls of which are

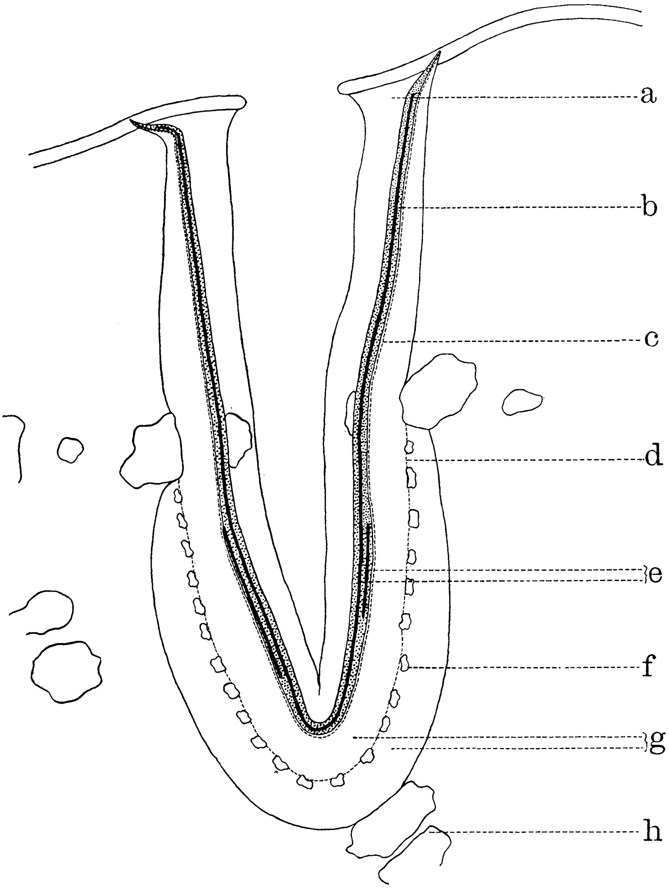

FIG. 3. Diagrammatic cross section through a thirty-one-day-old wound of an *Opuntia versicolor* plant, × 24. *a*, old tissue, bordering upon wound surface; very outermost cells are unchanged, others are discolored and their walls lignified; *b*, lignified thick-walled cells, produced by first wound-meristem; *c*, first wound-meristem; *d*, second wound-meristem; *e*, suberized thin-walled cells, produced by first wound-meristem; *f*, young vascular bundles produced by second wound-meristem; *g*, "phelloderm" tissue, produced by first and second wound-meristems, the cells being cellulose-walled, and containing small amounts of stored starch and oxalate crystals; *h*, old vascular bundles.

almost completely lignified. Bordering upon them is (3) the suberized phellem tissue, averaging four or five cells deep, below which are (4) the thick-walled lignin cells, usually two, but occasionally three deep. Inside is (5) more suberized tissue, which arises directly from (6) the phellogen. The phelloderm (7) below this, averages from ten to twelve cells deep, but is considerably thicker near the base of the "V," where the appearance of some of the cells seems to indicate the formation of a second meristem. The walls of the cells in this region are of cellulose, and the contents include small, probably newly formed oxalate crystals, and a considerable quantity of stored starch. The cortical cells (8) underneath the phelloderm have now practically regained their normal starch content.

TEXT FIG. 3 will aid in the study of a thirty-one-day-old wound. The periderm is more developed, and now includes in certain areas two more alternating layers of thick- and thin-walled tissue. However, the big advance made here comes in the further development of the second layer of meristematic tissue forming within the old periderm, parallel to the exposed surface. The function of this meristem seems to be to produce new vascular bundles.

These bundles develop first near the innermost portion of the wound, where the meristem was first seen to form. Küster (1, p. 164), in his discussion on the histology of callus, mentions the formation of tracheids, especially in the inner layer. By the union of many of these tracheids, he says, primitive vascular bundles, and a wood-like tissue are produced. However, here in the cacti, we have not just scattered rudiments of bundles, but distinct masses arranged in a definite position.

Eventually the first wound-meristem extends peripherally into the hypodermal tissue, but not until it is elsewhere very well developed. Another point to be noticed is that where the bundles were cut through, or where they are merely in a line with the wound phellogen, their prosenchymatic as well as their parenchymatic cells seem capable of reverting to a meristematic condition. Whether the stereome and hadrome tissues are able to revert is possibly questionable, but in these wounds it does not look as if the meristematic cells adjoining them had arisen from parenchyma cells some distance away.

DISCUSSION AND CONCLUSIONS

The series of changes which take place after injury, as described in the different ages of the wounds, really gives in itself a summary of what reactions took place.

The disappearance of starch in certain cells of the cacti prior to normal cork formation, is noted by Soraurer (5, p. 428), so it is not surprising to find it here, prior to the development of wound periderm, which, as can be seen, greatly resembles that produced normally.

This latter fact was noted by Schleiden (3, p. 353) who states that the best analogy to the natural cork building process is seen in the effect of wounding, and that this can be observed nowhere so easily as among the cacti. He does not, however, go greatly into detail, but describes the "drying up" of the cells on the surface of the wound, due to the "evaporation of their liquid contents" and says that this layer of "dried out" cells forms a protection to the cells underneath, out of which is formed the cork. He also states that the wound formation does not take place exclusively in cells exposed to air, but in behalf of this, gives no convincing proof.

Küster (1, p. 186) in his work on the histology of wound-cork, says that the walls are always thin, and often folded, and that differentiation of any kind whatsoever is entirely absent. This, of course, is not the case in these cacti. The formation of the thick-walled lignin cells is in itself enough to disprove the fact.

The essential new facts brought out by this paper are (1) the lignification of the old outer cortical cells, (2) the production of both thin- and thick-walled cells by the activity of the wound phellogen, and (3) the formation of the second interior meristematic layer, forming the new vascular bundles, parallel to the wound surface.

I wish to thank both Dr. D. T. MacDougal, of the Carnegie Desert Laboratory at Tucson, and Dr. H. M. Richards, of Barnard College, for their kindness in providing me with material, and to express my sincerest appreciation to Dr. Richards for the aid he has given me in my work.

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Explanation of plate 9

All figures are Zeiss camera lucida drawings from hand sections, which, with the exception of that shown in FIG. 5, were taken transversely through the stem. In some cases, as noted, the sections were stained to bring out the structures more clearly.

FIG. 1. Section through the hypoderm and epidermis of stem of an *Opuntia versicolor* plant, stained with Bismark brown, × 730. *a*, epidermis; *b*, outer layer of hypodermal cells, filled with calcium oxalate crystals; *c*, stomatal opening, leading down through hypodermal cells to cortical tissue; *d*, hypodermal cells; *e*, cortical tissue.

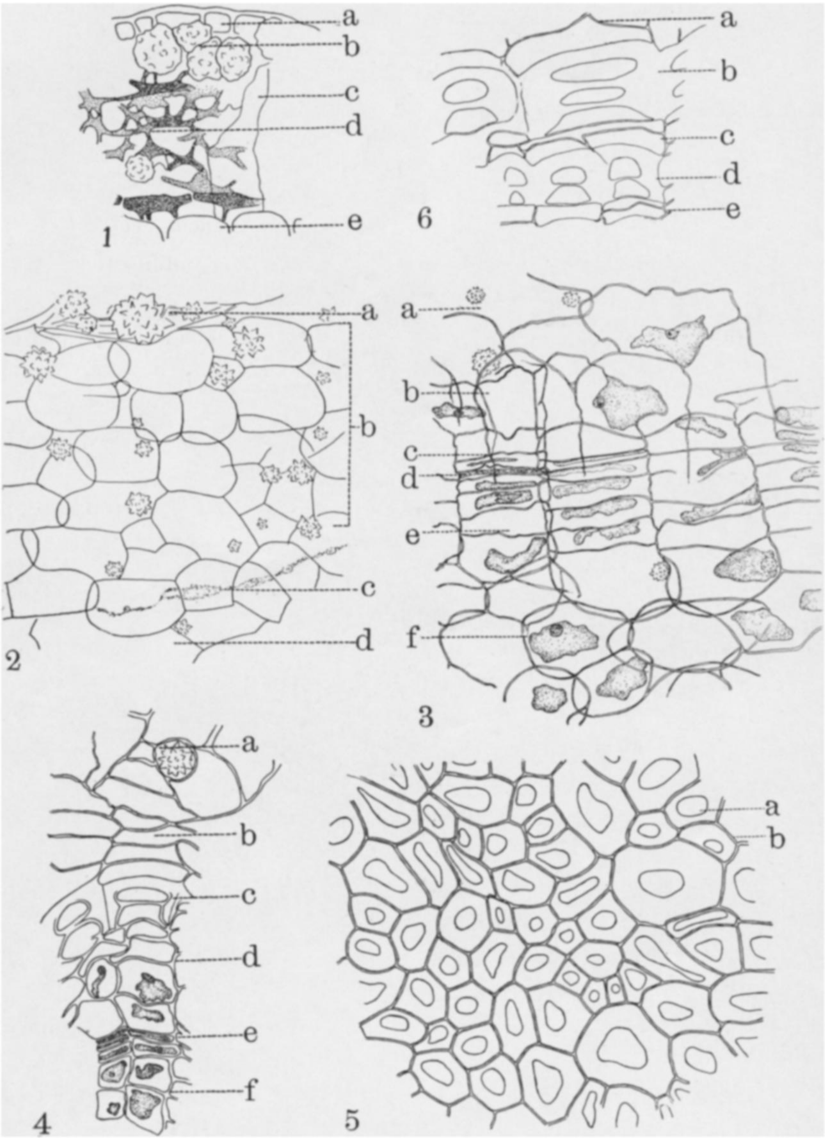
FIG. 2. Section taken near the periphery of a three-day-old wound in an *Opuntia versicolor* plant, × 245. *a*, cells bordering on wound surface which have retained their starch content; *b*, outermost portion of starchless layer, which has become somewhat discolored; *c*, cells which will later divide, and so form the first wound-meristem; *d*, inner portion of starchless layer.

FIG. 3. Section from near the periphery of a seven-day-old wound in an *Opuntia versicolor* plant, × 390, *a*, starchless cells, with lignified walls; *b*, starchless cells, the walls of which give test for both lignin and suberin; *c*, suberized-walled cells, which have arisen through the activity of the first wound-meristem; *d*, first wound-meristem; *e*, "phelloderm" tissue, produced by first wound-meristem; *f*, starchless cortical cells.

FIG. 4. Section through a twenty-four-day-old wound of an *Opuntia versicolor* plant, stained with Bismark brown, × 475. *a*, starchless cells, with lignified walls; *b*, outermost mass of suberized walled cells, produced through activity of first wound-meristem; *c*, lignified-walled cells, produced by first wound-meristem; *d*, inner mass of suberized-walled cells, produced through activity of first wound-meristem; *e*, first wound-meristem; *f*, "phelloderm" cells, produced by first wound-meristem.

FIG. 5. Transverse optical section of lignified-walled cells, produced through activity of first wound-meristem, stained with phloroglucin and hydrochloric acid, × 390, *a*, cell lumen; *b*, middle lamella.

FIG. 6. Portion of wound-periderm produced in an *Opuntia versicolor* plant, injured thirty-one days; all tissues shown have arisen from first wound meristem; stained with Bismark brown; × 475. *a*, outer mass of suberized thin-walled cells; *b*, outer mass of lignified thick-walled cells; *c*, middle mass of suberized thin-walled cells; *d*, inner mass of lignified thin-walled cells; *e*, inner mass of suberized thin-walled cells, arising from first wound-meristem (not shown).



COUTANT: WOUND PERIDERM IN CACTI